EXOSKELETAL MICRO-REMAINS OF AN ORDOVICIAN FISH FROM THE HARDING SANDSTONE OF COLORADO

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ABSTRACT. Three dimensional scales and fragments of the dermal skeleton from a hitherto little known fish have been isolated from the Ordovician Harding Sandstone of the type area around Cañon City, Colorado, USA, allowing exoskeletal morphology to be correlated with tissue structure and arrangement. Scales with a small crown sculpted into ridges over an extended base exhibit the same histology as material in bone-bed thin sections previously described as 'Vertebrate indet. A' by Denison (1967) and here formalized as *Skiichthys halsteadi* gen. et sp. nov. Possible taxonomic relationships with the osteostracans and primitive gnathostomes, elasmobranchs, acanthodians and placoderms are discussed. The microsquamous exoskeleton exhibits a variety of histological characters: enameloid, mesodentine with odontocytes, basal bone with osteocytes and numerous extrinsic fibre bundles in groups crossing at right angles and inserted at the visceral surface. The suprageneric assignment of *Skiichthys* is uncertain, but a taxonomic relationship to either the acanthodians or the placoderms is likely. The contemporaneous and co-occurring pteraspidomorph agnathans, *Astraspis* and *Eriptychius*, have an exoskeleton of plates and tesserae of acellular bone (aspidin) and tubular dentine and are not closely related to *Skiichthys*.

JAWED vertebrates, in the form of chondrichthyans and acanthodians, have long been thought to have unequivocal first records in the Silurian, but published studies seem to describe relatively advanced forms, rather than stem taxa which would offer firm evidence of phylogenetic links between the major groups of the gnathostomes and their supposed predecessors, the agnathans or jawless vertebrates. Two scenarios have been put forward to solve this problem. The first is that the acquisition of dermal armour occurred independently in the gnathostomes and agnathans, and that this was preceded by a period of diversification of fish lacking mineralized armour and consequently with low preservation potential (Carroll 1987). A second view suggested that the main period of diversification occurred during the Silurian and that 'the evolution of fishes was slow during the Ordovician' (Benton 1990, p. 45). Recent work on the middle Ordovician of North America has yielded data which enable a re-evaluation of these two hypotheses, and has led to the realization that many of the major groups of fish were already components of the marine fauna some 450 million years ago (Sansom *et al.* 1996).

Three-dimensional microvertebrate remains were recovered from the Harding Sandstone utilizing petroleum ether (following the methodology of Swift 1987). Sectioning of isolated scutes has enabled correlation with the classic diagnostic histologies observed in thin sections made from the bone bed horizons within the Harding Sandstone. We describe here a new morphology of micromeric scales, with histology identical to that of 'Vertebrate indet. A' (Denison 1967, p. 185), which forms the basis for *Skiichthys halsteadi* gen. et sp. nov. The characteristics of the distinctive histologies present in *S. halsteadi* are analysed and assessed in relation to higher order taxa, such as osteostracans, chondrichthyans, acanthodians and placoderms. The implications for tissue evolution and developmental models (Smith and Hall 1993) involving putative neural crest cells, already proposed for *Skiichthys* (Smith 1991), can be more realistically evaluated with the new analysis.

EARLY VERTEBRATE SKELETAL STRUCTURES AND CLADISTIC PHYLOGENIES

Currently accepted phylogenies propose that heterostracans are more primitive than osteostracans and Forey and Janvier (1994) predicted that bone without cells is the primitive vertebrate tissue, a point previously made by Janvier (1981, 1984). Given these hypotheses, it is important to try to establish the phylogenetic position of *Skiichthys halsteadi* as its skeletal tissues are characterized by the presence of cellular bone. The taxonomic position of *Skiichthys* is also crucial to the debate concerning the earliest occurrence of higher taxa, as well as for tissue evolution. Maisey (1988, p. 16) concluded that 'acellular bone is cladistically primitive', and stated that '…the earliest scraps of cellular bone are of uncertain affinity and consequently have no bearing on the present phylogenetic analysis'. Although Forey and Janvier (1994) concluded that cellular bone is an advanced feature, they also confused the issue by stating that 'the presence of cellular bone in the Ordovician vertebrates is an ancient trait of vertebrates' (p. 564). Blieck (1992, fig. 6) placed 'the third vertebrate of the Harding Sandstone' at the stem of clades leading to osteostracans and gnathostomes, in a stratigraphically constrained cladogram depicting early chordate relationships. It has, therefore, become imperative to describe fully the available material in order to assess phylogenetic relationships with other early vertebrates.

PREVIOUS INVESTIGATIONS OF ORDOVICIAN FISH

Examples of mineralized skeletal tissue of Ordovician fish with enclosed cell spaces are extremely rare and only those from the Harding Sandstone of Cañon City, Colorado, USA have been credited as representing cellular bone (Vaillant 1902; Stetson 1931; Ørvig 1951, 1965; Denison 1967; Smith and Hall 1990; Smith 1991). The agnathan taxa *Astraspis* and *Eriptychius* were first described from the Harding Sandstone by Walcott (1892). Subsequent histological studies have shown that the dermal denticles of these forms are characterized by acellular tissues (Bryant 1936; Ørvig 1965, 1989; Denison 1967; M. M. Smith *et al.* 1996; Sansom *et al.* 1997). Denison (1967, p. 185, fig. 26) described and figured sectioned denticles constructed of cellular 'dentine-like and bone-like tissues', characteristic of his 'Vertebrate indet. A'. Smith (1991, fig. 1C–D) identified a similar histology and figured sections of denticles of this Harding Sandstone vertebrate. Both cellular dentine and cellular bone were illustrated within the same denticle, the latter as basal flanges surrounding two, shallow, soft tissue invaginations. Neither Denison (1967) nor Smith (1991) were able to recognize these denticles macroscopically from the sectioned material of tissue retained *in situ* within the rock matrix, but Smith predicted from numerous random section planes of the denticles that the sculptured, enameloid covered crown was multi-crested or ridged and was smaller than, and eccentric to, the bony base. Denison (1967, p. 185) established that 'Vertebrate indet. A' was distinct from *Astraspis* and *Eriptychius* as it was 'constructed in part of a tissue similar to bone' but, while unable to refer it to any known group, he did conclude (1967, p. 186) that 'the mesodentine is most comparable to the superficial tissue of primitive Osteostraci'. Halstead Tarlo (1967) had independently concurred with this opinion, placing it in the Osteostraci, as a tremataspid without further discussion. Smith (1991, pp. 302–303) proposed that the species exhibited '…an early example of a primitively micromeric skeleton' and had both 'bone with osteocytes, and mesodentine with odontocytes' and was, therefore, possibly related to either the acanthodians or the osteostracans. Recently, de Ricqlès (1995, pl. 1, fig. 7) illustrated a specimen of Vertebrate indet. A 'with its base apparently ankylosed upon an aspidin'. However, similar specimens in our extensive new collections lack evidence of aspidin in the base.

Articulated Ordovician fish are extremely rare. The Harding Sandstone has yielded one partially articulated specimen of *Eriptychius americanus* Walcott (Denison 1967) and three incomplete specimens of *Astraspis desiderata* Walcott (Bryant 1936; Lehtola 1983; Elliott 1987; Sansom *et al.* 1997). Articulated specimens have also been described from Australia and Bolivia, but these offer little potential for histological work, being either sandstone moulds (*Arandaspis* and *Porophoraspis*; Ritchie and Gilbert-Tomlinson 1977) or weakly metamorphosed (*Sacabambaspis*; Gagnier *et al.*
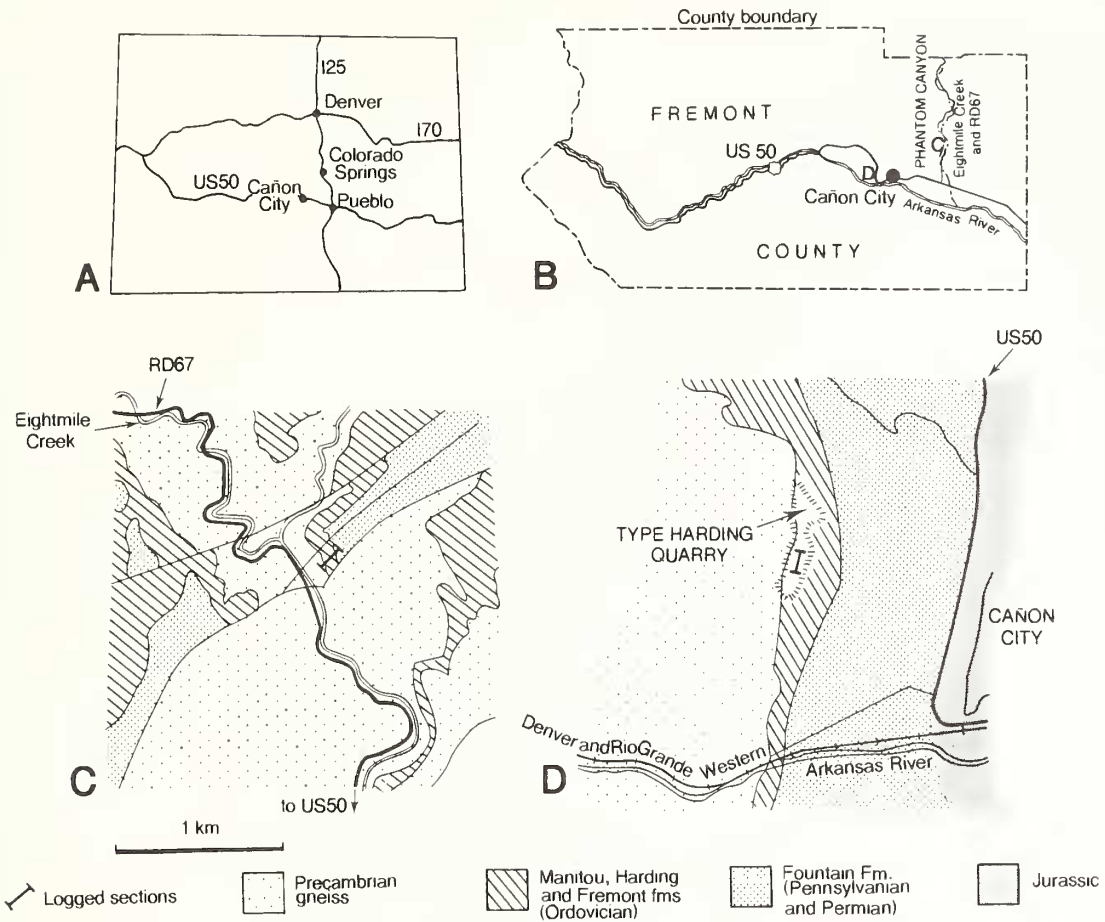
TEXT-FIG. 1. The *Skiichthys*-bearing localities. A, map of Colorado. B, map of Fremont County showing the relative locations of the Phantom Canyon section (C) and the Harding Quarry (D). C, geological sketch map showing the type section of *Skiichthys* in Phantom Canyon (adapted from Wobus *et al.* 1985). D, geological sketch map showing the type quarry for the Harding Sandstone (adapted from Taylor *et al.* 1975).

1986; Gagnier 1993). Disarticulated material, possibly related to *Arandaspis* and *Sacabambaspis*, from the Stokes Siltstone (Llanvirn) in Australia, offers some information on the arrangement of the tissues and their morphology (Gavin Young, pers. comm.), but definitive statements are precluded because of diagenetic alteration. The paucity of articulated remains of Ordovician fish with well-preserved histological features severely restricts the number of characters with which phylogenetic analyses may be made.

TYPE LOCALITY AND STRATIGRAPHY

The Harding Sandstone has its type area around Cañon City, Fremont County, east central Colorado (Text-fig. 1). The unit is dated on the basis of its locally abundant conodont fauna, which places the unit in the early Franklinian (*Phragmodus undatus* Chronozone of Sweet 1984) and correlatable with the lower middle Caradoc in British terms. Although the unit has sometimes been described as fluviatile (Graffin 1992) or estuarine (Fischer 1978), the overwhelming evidence, both palaeontological and sedimentological, is that virtually all of the sequence is marine (Spjeldnaes
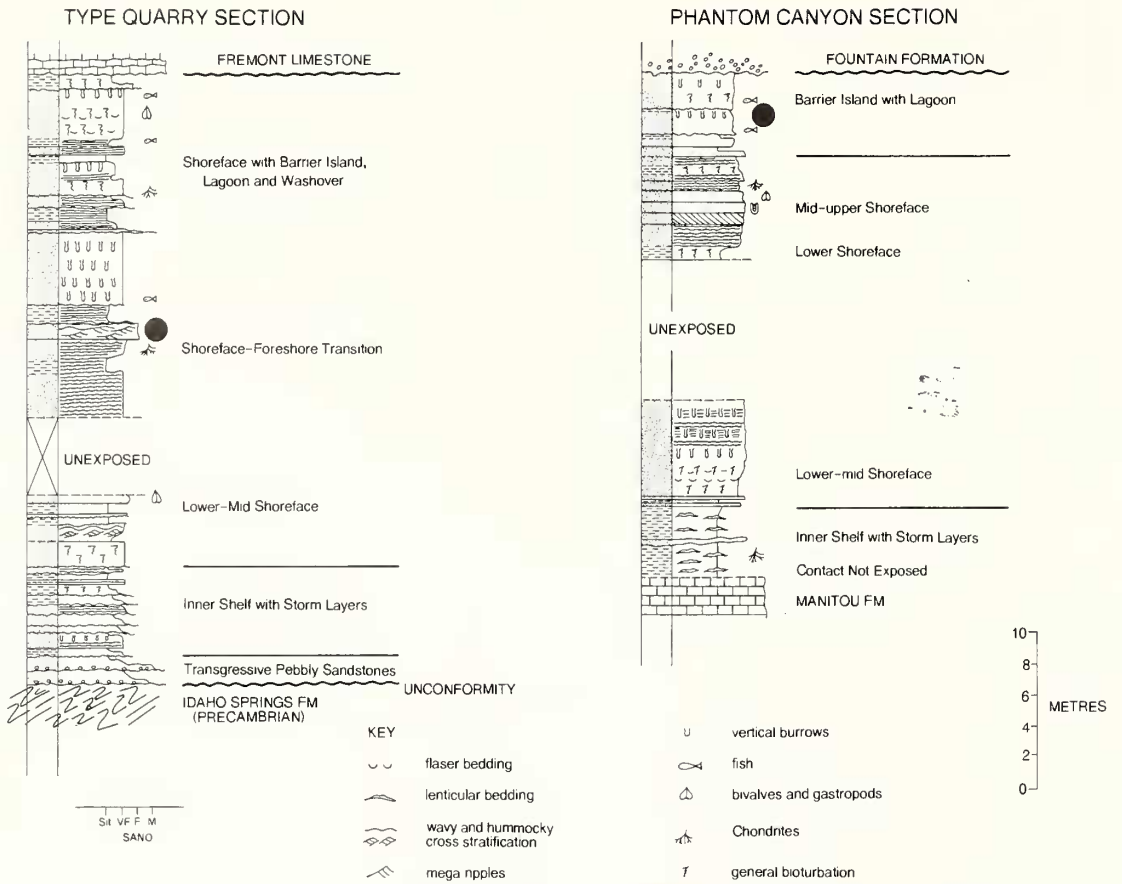
TEXT-FIG. 2. Sedimentary logs for the Phantom Canyon section and type Harding Quarry, together with a preliminary sedimentological interpretation. Dots indicate beds known to yield *Skiichthys* specimens. Logs made and interpreted by Dr Peter Turner (University of Birmingham).

1967). In the type area, the Harding Sandstone is characterized by sandstones and siltstones, which represent five or six parasequences representing inner shelf to shoreface transitions, possibly representing part of a barrier island complex (Text-fig. 2; Turner *et al.* 1994).

The Harding Sandstone has a far more diverse fish fauna than has been hitherto documented, and a preliminary study of the palaeoecology of the unit suggests that subtly different palaeo-environments supported disparate communities of fish. *Skiichthys halsteadi* has been recorded from the Harding Quarry and a section sampled along Phantom Canyon, 1·5 km due west and 8 km north-east of Cañon City respectively (Text-fig. 1). Our preliminary palaeoenvironmental interpretation of the horizons containing *Skiichthys* suggests that the genus lived in extremely shallow water (Text-fig. 2), close to the strandline, and formed a relatively minor part (generally less than 5 per cent.) of a community dominated by *Astraspis* and *Eriptychius*. The scales of sharks, thelodonts (figured by Sansom *et al.* 1996) and as yet unassignable fish, plus conodont elements, complete the vertebrate fauna of the whole Harding Sandstone palaeoenvironment.

Institutional abbreviation: BU, Lapworth Museum, University of Birmingham, Birmingham, UK.

SYSTEMATIC PALAEONTOLOGY

Superclass GNATHOSTOMATA Cope, 1889?
Class INCERTAE SEDIS
Order INCERTAE SEDIS
Family INCERTAE SEDIS

Genus SKIICHTHYS gen. nov.

Derivation of name. From *skia* and *ichthys* (both Greek) for phantom fish, after the type locality in Phantom Canyon, and the elusiveness of three-dimensional material.

Type species. Skiichthys halsteadi gen. et sp. nov.

Diagnosis. The diagnosis follows that of the type and only species, given below.

Skiichthys halsteadi sp. nov.

Plate 1; Text-figures 3–4

v 1967   Vertebrate indet. A Denison, p. 184, fig. 26.
v 1991   'vertebrate indeterminate A' Denison; Smith, figs 1–3.
v 1995   Vert. Indet. A, Smith *et al.*, pl. 1, figs 5–6.
v 1995   Indeterminate Vertebrate A of Denison; de Ricqlés, pl. 1, figs 1–5, 7.
v 1996   Vertebrate indet. A of Denison; M. M. Smith *et al.*, fig. 2D–F.

Derivation of name. After Beverly Halstead who inspired the histological evaluation of this material and made a considerable contribution to the debate on primitive bone-like tissues.

Type locality. Harding Sandstone, Phantom Canyon (lat. 38° 30′, long. 105° 06′), north-east of Cañon City, Colorado (Text-figs 1–2).

Holotype. Isolated scale, BU 2599.

Diagnosis. Fleur-de-lys ornamented scales with markedly flared bases, showing non-areal growth and lacking neck canals, and formed from enameloid, mesodentine and cellular bone.

Description. Minute, individual scales are ovoid, 0·18–2 mm across the base, each with a distinctive *fleur-de-lys* ornamented crown above a more extensive flared base (Text-fig. 3) and without neck canals. The small crown, eccentric on the base, has a central high ridge, flanked by two lower, sub-parallel ridges with shallow furrows between, the three together form a *fleur-de-lys* shape. Some specimens have grooved and botryoidal ornament on these diagnostic ridges (Text-fig. 3F). The ridges of the tubercle are composed of, and shaped by, enameloid, which is confined to the upper part of the tubercle (Text-fig. 4). There is no prominent, organized vascular canal system in the crown, but irregularly arranged dentine canals, possibly containing vascular tissue, predominate in some of the more central regions of the dentine (Text-fig. 4). The bases of smaller, presumably juvenile, scales often have two or more shallow, wide open, soft tissue chambers, opening on the basal surface (pulp cavities; Pl. 1, fig. 1; Text-fig. 4), but the tubercle is without an extensive pulp cavity. A few of the larger scale bases have several enclosed vascular spaces; the surrounding tissue is cellular bone. Known only from microremains, the exoskeleton is microsquamous and the crown is non-growing. The basal bone increased in area after the odontodes formed, but no new odontodes were added. Larger tesserae have not been found, nor any with multiple tubercles on the base.

The superficial, refractile layer of the crown, a type of enameloid about 20–25 μm thick, is translucent and penetrated by numerous, sub-parallel tubules of similar dimensions to those in the dentine (Pl. 1, figs 1–3; Text-fig. 4). The junctional zone at the base of the cap enameloid, where it abuts the dentine, has short, broad tubules branching into the finer tubules that traverse the enameloid to the surface. The subjacent dentine tissue is more extensive and grades into the basal bone tissue; both have cell body-sized lacunae within the tissue (Pl. 1, figs 1–3, 5; Text-fig. 4). The lacunae of the dentine are pear-shaped spaces, leading into one or two directional

tubules which continue upwards into an extensive branching network of fine tubules ramifying throughout the dentine. A more concentrated network occurs in a marginal zone just below the enameloid, where some tubules continue across this junction. Faint lines occur in the coronal dentine, indicating the centripetal growth pattern of the tissue (Pl. 1, fig. 1; Smith 1991, fig. 1A–B). This tissue is most typical of mesodentine, a tissue with enclosed odontocyte lacunae and a few directional tubules, all linked by an extensive network of fine branches.

The most basal tissue, continuous with the dentine but extending beyond the base into broader flanges (Pl. 1, figs 1, 5; Text-fig. 4; Smith 1991, fig. 1c), has stellate lacunae with the points extending into canaliculi, these ramify throughout this region in an irregular arrangement linking the lacunae. Some of these canaliculi lead into the shallow cavities opening at the base, and the enclosed vascular spaces. This tissue arrangement is distinctive for the high density of osteocytic lacunae linked by a network of canaliculi, typical of true cellular bone.

All of the basal, cellular tissue has a matrix of broad fibre bundles, closely spaced and running radially from the base towards the crown (Pl. 1, fig. 4; Text-fig. 4). In many section planes, when viewed in polarized light, two sets of these fibres can be observed passing at right angles to each other (Pl. 1, fig. 6). This arrangement is regarded as comparable to the extrinsic matrix fibres of the attachment regions of bone or cementum in scales and teeth. This tissue is assumed to have served to attach these scales to the soft tissue of the dermis.

None of the specimens shows evidence of tesserae or compound scales. The basal tissue varies greatly in amount amongst the scales and has an irregular shape, but always extends beyond the area of the crown (Pl. 1, figs 1, 4). The superficial, glassy layer is thickest over the crests of the ridges, where it contributes to the surface sculpturing and tapers down over the surface of the dentine (Pl. 1, figs 1, 3; Text-fig. 4; Denison 1967, fig. 26A–B; Smith 1991, fig. 1A–C), the tubules within the enameloid are continuous with those of the dentine below, itself with a network of tubules as in mesodentine.

IMPLICATIONS FOR MODELS OF EVOLUTION OF THE DERMAL SKELETON AND POSSIBLE RELATIONSHIPS OF *SKIICHTHYS*

The scales of *Skiichthys* are both distinctive and remarkable for the possession of cellular bone and cellular dentine at a stratigraphically early, and morphologically simple (microsquamous), stage of skeletal organization of the dermal armour. The observation that cellular bone and cellular dentine co-occur suggests that they developed together within the odontogenic complex. In *Skiichthys* it is clear that they do not represent products of an evolutionary transition series from bone to dentine, as has been suggested previously (for reviews see Ørvig 1967, pp. 49–54; 65–79; 97–103; Smith and Hall 1990, p. 324).

In the absence of further information on the body plan of *Skiichthys*, the histology and morphology of the scales assumes a principal role in assessing the phylogenetic relationships of the taxon. The presence of mesodentine and cellular bone are of particular significance, and enable a number of primitive vertebrate groups to be excluded from this discussion.

Figs 1–6. *Skiichthys halsteadi* gen. et sp. nov.; Harding Quarry, Cañon City, Fremont County, Colorado, USA; Harding Sandstone, Caradoc. The histology of scales from random section planes of the bone bed material; figs 1–3, 5, taken in Nomarski differential interference contrast optics; figs 4, 6, taken in polarized light (polarizer N–S). 1, BU 2608; ortho-transverse vertical section of complete scale crown and partially developed base (arrows a–c show enameloid-dentine junction and two parallel growth contours of the dentine; asterisks mark the vascular cavities). 2, BU 2609; enameloid dentine junction is oblique; tubules in enameloid are continuous with those of the mesodentine; odontocyte lacunae are pear-shaped with coronally directed tubules. 3–4, BU 2610. 3, higher magnification of the crown tissue; enameloid covering with tubules; mesodentine with a marginal network extending from tubules of odontocyte lacunae below. 4, scale with more extensive base in which the direction of Sharpey's fibre bundles is shown by their birefringence as normal to the basal surface. 5, region of the base (close to asterisk in fig. 4) in which osteocytic lacunae and canaliculi are seen in addition to the Sharpey's fibre bundles. 6, BU 2611; example of an extensive scale base sectioned in a plane which shows the alternating, opposite direction of Sharpey's fibre bundles in polarized optics. Figs 1, 4, × 190; figs 2–3, 5, × 480; fig. 6, × 75.

PLATE 1

SMITH and SANSOM, *Skiichthys*
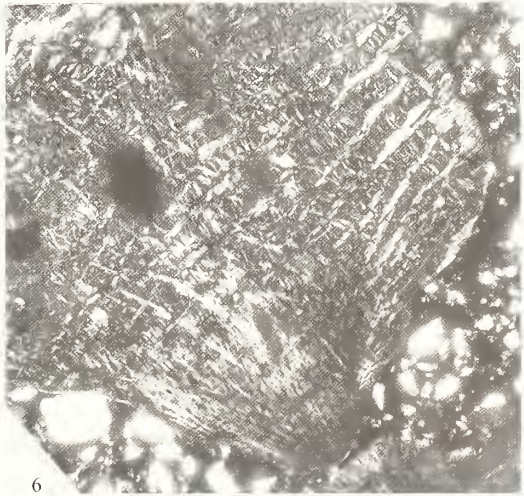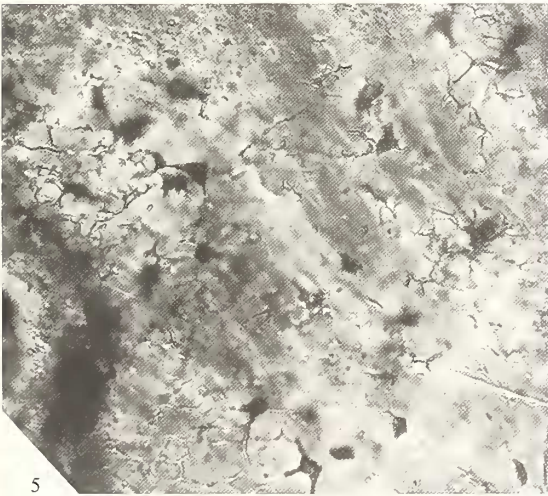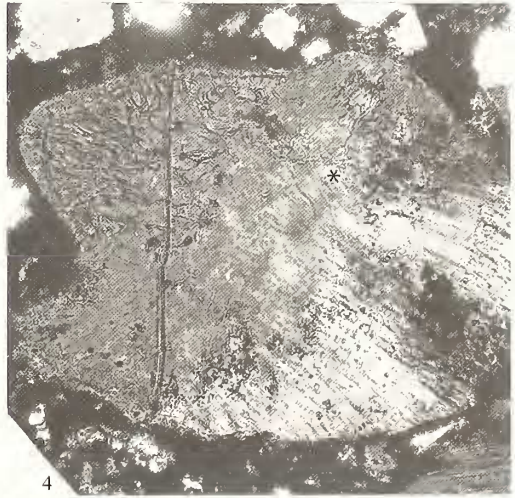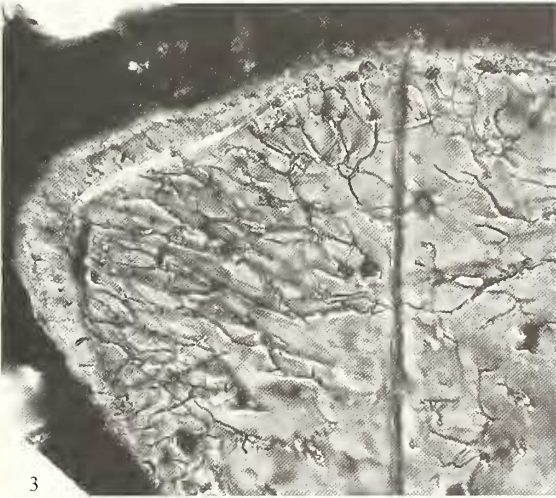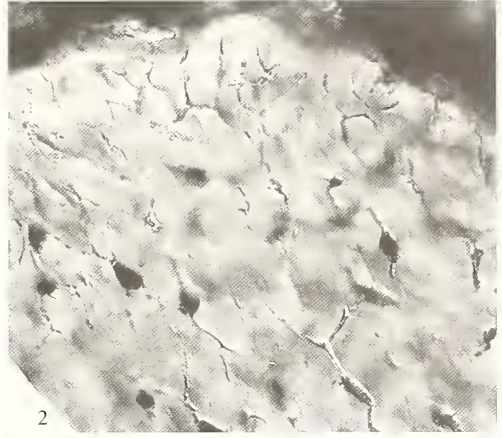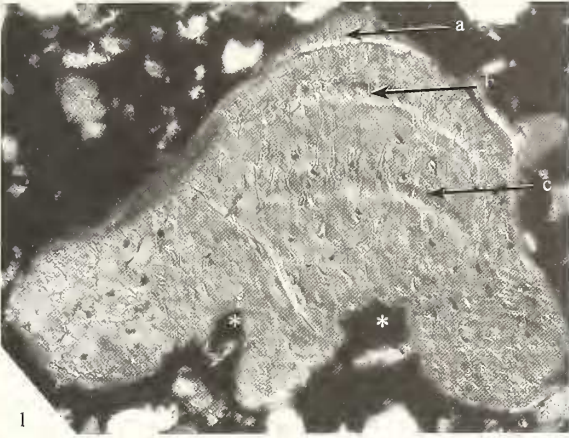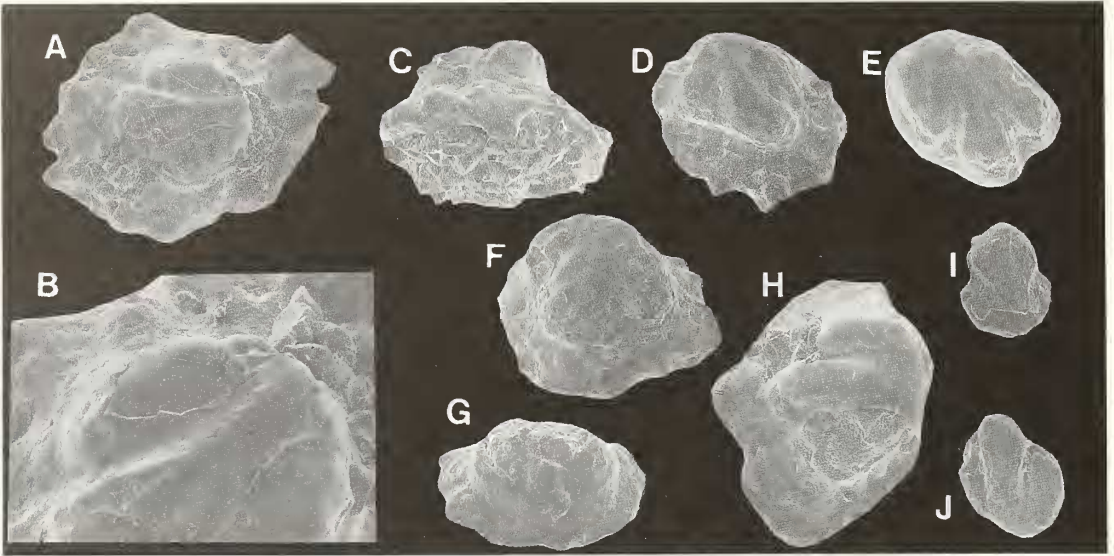
TEXT-FIG. 3. *Skiichthys halsteadi* gen. et sp. nov. A–H, Phantom Canyon, Fremont County, Colorado, USA; Harding Sandstone, Caradoc. A–B, BU 2599, holotype. A, dorsal view; B, detail of cap region where the enameloid has broken away, revealing diagenetically infilled dentine tubule network of the underlying mesodentine. C, BU 2600; lateral view. D, BU 2601; dorsal view. E, BU 2602; dorsal view of specimen with weakly developed base. F, BU 2603; dorsal view of unusual specimen showing botryoidal ornament on *fleur-de-lys* cap. G, BU 2604; dorsal view. H, BU 2605; dorsal view. I–J, Harding Quarry, Cañon City, Fremont County, Colorado, USA; Harding Sandstone, Caradoc; dorsal views of abraded specimens, typical of the preservation seen in material from the type Harding Quarry. I, BU 2606; J, BU 2607. All ×24 except B, ×56.

Ordovician pteraspidomorphs

Astraspis and *Eriptychius*, which co-occur with *Skiichthys* in the Harding Sandstone, have dermal armour formed from acellular bone (aspidin) overlain by tubercles of acellular dentine. However, it is noteworthy that the superficial enameloid of *Skiichthys* is similar to the enameloid found over stellate denticles of *Astraspis*, although it never shows the thickness developed in the larger, mushroom-shaped tubercles also seen in the latter genus (vitrodentine, Denison 1963, p. 145; durodentine, Denison 1967, p. 174). The junctional zone in *Skiichthys*, where enameloid overlies the dentine below, reveals short wide tubules giving rise to several finer branches, many of which lead to the surface of the enameloid. This is identical to the equivalent region in the tubercles of *Astraspis*, figured by Ørvig (1958, fig. 3; 1989, figs 16–18). He interpreted this junctional layer as one with scleroblast cell bodies related to the formation of the outer layer. Ørvig (1958) initially thought that this layer represented the remains of true dentine in *Astraspis*, as he regarded the main tissue of the tubercle as aspidin. Subsequently, Ørvig (1989) considered the junctional layer to be comparable to the ascending dentine canals topped by clusters of branching tubules in katoporid thelodonts and heterostracans, and to the mesodentine of early osteostracans. The junctional layer has also been figured in *Astraspis* by M. M. Smith *et al.* (1996, fig. 1B, E), and Sansom *et al.* (1997), who interpreted the wide tubule spaces as being related to the formation of enameloid, while the dentine below retained another set of cell processes, some of which continue into the enameloid.

Gagnier (1993) noted that the dermal armour of *Sacabambaspis* appeared to lack dentine. Although ovoid lacunae within the hard tissues of *Sacabambaspis* were interpreted as cell spaces, they lack cell processes and bear little resemblance to the cellular bone of *Skiichthys*.

1mm
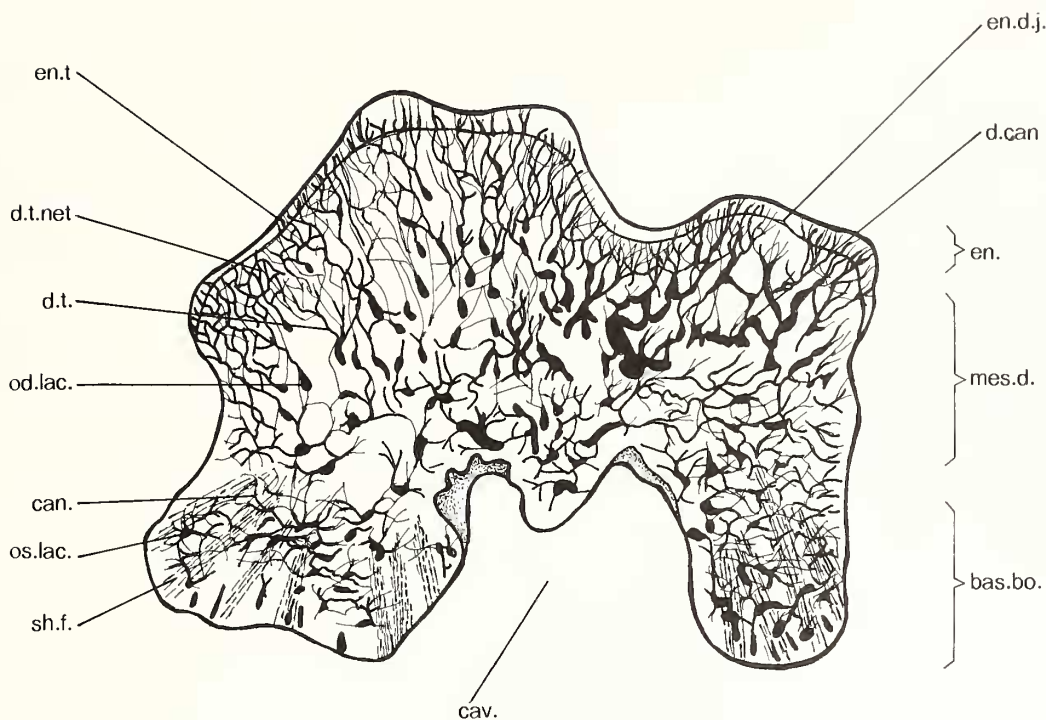
TEXT-FIG. 4. Vertical section through the crown and base of a *Skiichthys halsteadi* gen. et sp. nov. scale, BU 2607, to show the characteristic tissue types, their arrangement and proportions. The crown is mesodentine covered by enameloid, a system of dentine canals is located centrally, and odontocyte lacunae give rise to tubules which terminate in a marginal network and also extend into the enameloid. The base has numerous osteocytic lacunae and canaliculi forming an irregular network, the matrix has many Sharpey's fibre bundles radiating from the visceral surface. Abbreviations: bas.bo., basal bone; can., canaliculi; cav., soft tissue vascular cavity; d.can., dentine canals; d.t., dentine tubules; d.t.net., dentine tubule network; en., enameloid; en.t., enameloid tubules; en.d.j., enameloid dentine junction; mes.d., mesodentine; od.lac., odontocyte lacunae; os.lac., osteocyte lacunae; sh.f., Sharpey's fibre bundles.

Thelodonts

Thelodonts are characterized by discrete, non-growing scales, with distinctive varieties of dentine. All the thelodonts have very weakly developed bases. *Sandivia melnikovi* Karatajūte-Talimaa, 1997, a loganiid thelodont from the Ashgill of Timan-Pechora Province, Russia, and an as yet un-named taxon recovered from the Harding Sandstone (Sansom *et al.* 1996) represent the known records of thelodonts from the Ordovician. Neither of these forms resembles *Skiichthys* in morphology or histological character.

Osteostracans

Denison (1967, p. 185) suggested that the mesodentine seen in *Skiichthys* was 'most comparable to the superficial tissues of primitive Osteostraci', although he did not feel that this was sufficient evidence to assign the taxon to the osteostracans. The presence of cellular bone in *Skiichthys* and the majority of osteostracans would seem to lend support to a phylogenetic relationship. However,

Skiichthys differs from osteostracans in a number of notable features. We have yet to recover large fragmentary plates carrying the multiple tubercles that would be likely if *Skiichthys* was an osteostracan with a headshield, the preservational potential of which would be high. The scales we have recovered do not show any evidence for the development of tesserae. The osteostracans are characterized histologically by the presence of a continuous superficial layer of dentine and enameloid, containing a pore-canal system (Janvier 1996, pp. 107, 112). *Skiichthys* lacks an organized vascular system, although there are irregularly arranged canals in some areas of the mesodentine. Well-developed attachment fibres are present in *Skiichthys*, but attachment fibres have yet to be described in published accounts of osteostracan histology. In addition, there is no evidence for the presence of any endoskeletal material associated with *Skiichthys*.

The micromeric condition of *Skiichthys*, together with the absence of a well-developed pore-canal system, 'definitively characteristic of the Osteostraci' (Denison 1951, p. 200), would appear to rule out an assignment to this group.

Chondrichthyans

Ørvig (1966) has described mesodentine in the teeth and scales of an elasmobranch *Holmesella* sp. from the Upper Carboniferous of South East Kansas, USA (1966, p. 24, fig. 3B, pl. 5), and added that 'this is a retained primitive character not found in other elasmobranchs'. However, descriptions of the earliest chondrichthyans, including *Elegestolepis grossi* Karatajūte-Talimaa, 1973 from the Upper Silurian of Tuva, *Elegestolepis conica* from the Lower Silurian of Siberia (Karatajūte-Talimaa and Predtechenskyj 1995), and an as yet un-named polyodontode form from the Harding Sandstone (Sansom *et al.* 1996), show dentine with many branching wide and narrow tubules, generally lacking lacunae, and best described as 'arboriform' tubular dentine. Although some examples of mesodentine have been described in *Elegestolepis* scales (Karatajūte-Talimaa 1973, figs 2C, E, 3A–B), and a few lacunae are present in the basal tissue, they were later described as orthodentine (Karatajūte-Talimaa and Predtechenskyj 1995, fig. 8B–F) and the tissue arrangement and morphology are quite different from those of *Skiichthys*. In *Elegestolepis* the crown is non-growing but tissue was added centripetally to the pulp chamber and centrifugally to the small base.

Stratigraphically early elasmobranch scales from the Upper Lochkovian, Ellesmere Island, Northwest Territories, Canada, have been described with irregular branching dentine canals but no mesodentine, although in places there is a network of tubules. There are, however, no enclosed cell lacunae within this tissue (Vieth 1980).

Closely related to the chondrichthyans are *Mongolepis rozmanae* Karatajūte-Talimaa, Novitskaya, Rozman and Sodov 1990 and *Teslepis jucunda* Karatajūte-Talimaa and Novitskaya 1992, from the Lower Silurian of Western Mongolia. These taxa have a very distinctive crown morphology made of an atubular dentine termed lamellin. The base in the latter species is composed of bone with fusiform lacunae but lacking interconnecting canaliculi. These two species again do not have morphological or histological characters in common with *Skiichthys*; most notably their scales are formed from polyodontodes; nor do the other elasmobranch scales, discussed above, compare closely in their histology, morphology or mode of growth.

Placoderms

Mesodentine similar to that seen in *Skiichthys* has been illustrated in the rhenanid placoderm *Ohioaspis tumulosa* Wells (Gross 1973, fig. 2D, F–G). Ørvig (1975, pl. 8, fig. 1, p. 44) also figured and described mesodentine in an acanthothoracid arthrodire, *Romudina stellina* Ørvig; he commented that this is one of the few occurrences in arthrodires of a tissue similar to the mesodentine of osteostracans. Mesodentine is also present in the coronal tissue of tuberculate scales and small tesserae of *Radotina* sp. from the Lochkovian of Podolia, another micromeric acanthothoracid. These microskeletal remains, together with sections of tesserae of *Ohioaspis* and *Romudina*, have been compared with those of *Skiichthys* and the tissue mesodentine found to be similar in all (MMS and Karatajūte-Talimaa, pers. obs.). Osteocytic bone in these forms is also predominant in the

middle layer. However, in the placoderm scales there is an obvious system of horizontal canals and pulp cavities, not found in *Skiichthys*, and in those of *Romudina* there is also a layer of spongy bone. Small scales and thin, non-overlapping tuberculate tesserae may be primitive for all placoderms (Denison 1978), as may be mesodentine. As with the osteostracans, *Skiichthys* may be excluded from the placoderms on the absence of any multi-tuberculate tesserae in our collections.

Acanthodians

The tissues of *Skiichthys* share a number of histological features with an undescribed acanthodian from the Middle Llandovery of the Siberian Platform (Karatajūte-Talimaa, pers. comm.) and the Climatiidae, thought to be close to the ancestral shock of Acanthodii (Denison 1979; Long 1995). These include: the presence of mesodentine in the crown (e.g. *Nostolepis* Pander; Gross 1971, figs 2E, 12F, 17M, 18B; and *Euthacanthus* Powrie; Denison 1979, fig. 10A); radially arranged extrinsic Sharpey's fibres in the basal bone; and the presence of bone and dentine with enclosed cell body lacunae interconnected by a network of canaliculi and branching tubules (seen in the undescribed Siberian genus, in *Euthacanthus* and in the ischnacanthid *Gomphonchus* Gross, 1971, fig. 22D). However, the scales of *Skiichthys* differ in not showing strong evidence of areal growth, although in *Euthacanthus* scale growth is only appositional and not superpositional.

Members of the Climatiidae retain many assumed primitive characters, and are thought to be close to the ancestral stock of the Acanthodii (Denison 1979; Long 1995). Among these primitive characters are: a head and trunk covered with small scales, none enlarged, all ornamented by three or four short, converging ridges, superficial mesodentine with no Stranggewebe and a flat base of cellular bone, a pulp-like cavity with no radial canals, and only a little overgrowth in one lateral zone. In *Euthacanthus* (Denison 1979, fig. 10A) the primordial scale is large, backwardly sloping, and added to by a single growth zone which is mainly expressed laterally. The phylogenetic significance of the lack of evidence for areal growth zones and an organized system of radial canals in *Skiichthys* could be considered as a primitive state for acanthodians. The presence of bone cell spaces (osteocytes), dentine cell spaces (odontocytes) and an interconnecting network of cell process spaces, which terminates in the enameloid, are considered as primitive characters of acanthodians, as is the absence of tubules organized into Stranggewebe (Denison 1979).

Larger scales of *Skiichthys* differ from those of all acanthodians described thus far in the presence of vascular spaces enclosed by cellular bone (not aspidin, *contra* de Riqles 1995). The lack of enclosed vascular spaces in later acanthodians either argues against a firm assignment of *Skiichthys* to this taxon, or that the presence of such a vascular system represents the most primitive state for the Acanthodii.

Micromeric condition

The radially arranged coarse fibre bundles in the base of *Skiichthys* (Pl. 1, figs 4, 6; Text-fig. 4), leading from the basal surface into the body of the scale, are similar to those seen in acanthodians (examples include *Gomphonchus* Gross, 1971, fig. 22D; *Diplacanthus* Agassiz; Denison 1979, fig. 10F; *Acanthoides* Agassiz; Denison 1979, fig. 10K), placoderms (e.g. *Ohioaspis tumulosa* Wells; Gross 1973, figs 2A, 7B) and elasmobranchs (e.g. *Hohnesella* Gunnell; Ørvig 1966, fig. 2A, pl. 4). These sets of extrinsic fibres functioned as an attachment mechanism, between the scale and the soft tissue of the dermis, known in many hard tissues as Sharpey's fibres, and are a common feature of micromeric scale bases. The progressive mineralization of these attachment fibres was part of the growth process in the basal bone.

CONCLUSIONS

The firm taxonomic assignment of *Skiichthys* depends upon the recovery of articulated remains, or larger fragments, such as spines or tesserae. The available histological and morphological evidence suggests that *Skiichthys* is not an early osteostracan, but could represent a plesion of either the placoderms or acanthodians. Alternatively, *Skiichthys* may represent a new micromeric group,

probably within the gnathostome clade. However, as is the case for the contemporaneous shark-like denticles described from the Harding Sandstone by Sansom *et al.* (1996), the absence of positive evidence for the presence of jaws and teeth in *Skiichthys* prevents a definitive assignment to the gnathostomes.

The dermal skeleton of *Skiichthys* is formed principally from cellular mesodentine and cellular bone. These are not the stratigraphically earliest vertebrate hard tissues, Ordovician ptera-spidomorphs have acellular aspidin and tubular dentine in their dermal armour, as exemplified in *Astraspis* and *Eriptychius* from the same locality. The demonstration of the Late Cambrian *Anatolepis* Bockelie and Fortey as the earliest non-conodont vertebrate (M. P. Smith *et al.* 1996) implies that acellular tissues are primitive for vertebrates.

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